PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
116(2):380–394. 2003.

On the occurrence of the vestimentiferan tube worm *Lamellibrachia luymesi* van der Land and Nørrevang, 1975 (Annelida: Pogonophora) in hydrocarbon seep communities in the Gulf of Mexico

Stephen L. Gardiner and Stéphane Hourdez

(SLG) Department of Biology, Bryn Mawr College, 101 N. Merion Avenue, Bryn Mawr, Pennsylvania 19010, U.S.A.;
(SH) The Pennsylvania State University, Department of Biology, 208 Mueller Laboratory, University Park, Pennsylvania 16802, U.S.A.

Abstract.—*Lamellibrachia luymesi* van der Land & Nørrevang, 1975 is recorded from shallow-water hydrocarbon seep communities along the Louisiana slope in the Gulf of Mexico. It is typically the most abundant tube worm species in these shallow-water communities, sometimes with individuals occurring in aggregations numbering in the thousands. Tubes extend deeply into the sediment, and apical portions may project above the sea floor a distance of one meter or greater. This study documents intraspecific variation for a number of important morphological features of *L. luymesi,* such as the number of sheath lamellae, the number of branchial lamellae, the length and width of the obturaculum and vestimentum, the ratio of obturacular length to vestimental length, the ratio of vestimental diameter to vestimental length, and features of the tube. Comparisons of these features are made with other species of *Lamellibrachia.* The record of *L. luymesi* on the Louisiana slope extends the geographic range of this species from the southern North Atlantic Ocean into the northern Gulf of Mexico.

Subsequent to the description of the first species of *Lamellibrachia, L. barhami,* by Webb (1969), van der Land & Nørrevang (1975) described a second species, *L. luymesi,* and discussed the possible relationships that vestimentiferans in general have with the Annelida, Polychaeta, and Pogonophora. Following their original description, van der Land & Nørrevang (1977) provided an in-depth description of the anatomy and histology of *L. luymesi.* Both the original description and the subsequent anatomical and histological account were based on a single male specimen collected off the coast of Guyana in about 500 m of water.

The record of *L. luymesi* off the coast of Guyana remained as the only documented vestimentiferan species from the Atlantic Ocean until Paul et al. (1984) reported the presence of vestimentiferan tube worms in 3000 m of water at the base of the Florida Escarpment in the Gulf of Mexico which were later named *Escarpia laminata* by Jones (1985). A second Atlantic species of *Lamellibrachia, L. victori,* was described by Mañé-Garzón & Montero (1985), based on two specimens collected in about 300 m of water off Uruguay. Since the description of *L. victori,* no additional confirmed records of either Atlantic species of *Lamellibrachia* have been published. However, beginning in 1985 (Kennicutt et al. 1985), numerous records of a *Lamellibrachia* sp., occurring along the Louisiana slope in the Gulf of Mexico, have been reported (see synonymy below).

The purpose of the present study is to confirm the identity of the *Lamellibrachia* sp. that occurs along the Louisiana slope as

L. luymesi and to provide an account of the intraspecific variation it displays with regard to certain important diagnostic morphological characters.

Systematics

As discussed in Gardiner et al. (2001), the systematic relationships of vestimentiferans remain unsettled. In order to maintain consistency with other recent descriptions of vestimentiferans and broader discussions of pogonophoran morphology and phylogeny (Southward et al. 2002, 2003), we consider vestimentiferans as comprising a subclass within the class Pogonophora of the phylum Annelida.

Materials and Methods

Specimens were collected by the manned submersible *Johnson-Sea-Link I (JSL I)* from two hydrocarbon seep sites on the Louisiana slope in the Gulf of Mexico and brought to the surface in a temperature-insulated container. On board ship, specimens were immediately fixed in their tubes in 10% buffered formalin in seawater. In the laboratory, tubes were sliced open with the aid of a Dremel Moto-Tool high speed drill, and specimens were extracted, rinsed in distilled water and transferred to 70% ethanol.

For scanning electron microscopy (SEM), materials were dissected from selected specimens, dehydrated in a graded ethanol series, critical-point dried, using carbon dioxide, and sputter coated with gold-palladium. Material was examined in either a Topcon ABT-60 or a JEOL JSM-5200 scanning electron microscope. Negatives of figures were scanned at 600 dpi, and plates were constructed using Adobe Photoshop 7.0 (Adobe Systems, Inc., San Jose, California, USA).

Subclass Vestimentifera Webb, 1969
Family Lamellibrachiidae Webb, 1969
Genus *Lamellibrachia* Webb, 1969

Type species.—Lamellibrachia barhami Webb, 1969, by monotypy.

Diagnosis.—Vestimentiferan worms with tapering tubes and bodies. Anterior obturacular region provided with branchial plume; orientation of branchial lamellae relative to obturaculum axial and parallel; branchial filaments of obturacular plume of one type; plume covered by variable number of peripheral sheath lamellae; anterior face of obturaculum bare, lacking crust or secreted structures; paired internal excretory ducts opening by single, dorsal medial excretory pore. Anteroventral margin of vestimentum discontinuous, posteroventral margin of vestimentum broadly discontinuous, lobes usually not overlapping. Opisthosome with variable number of segments; chaetigerous segments with chaetae usually in single row; chaetae with variable number of teeth in anterior and posterior groupings. Tube hard, tapered, usually with variable number of collars anteriorly, becoming smooth posteriorly (Webb 1969; van der Land & Nørrevang 1975, 1977; Jones 1985; Southward 1991).

Lamellibrachia luymesi van der Land & Nørrevang, 1975
Figs. 1–8

Lamellibrachia luymesi van der Land & Nørrevang, 1975:86–101, Figs. 1–7; 1977:1–102, pls. 1–26.—Jones, 1985: 128.—Southward, 1991:872–874, table 2.

Lamellibrachia sp.—Kennicutt et al., 1985: 351, 352, table 1.—Childress et al., 1986: 1307.—Brooks et al., 1987:1139, table 1.—MacDonald et al., 1989:235–245, Fig. 3A–D.—Fisher et al., 1990:1095, table 1.—MacDonald et al., 1990:246, Fig. 2.—Childress & Fisher, 1992:382.—Williams et al., 1993:439, 440, table 1.—Carney, 1994:150.—Scott & Fisher, 1995:107, 109, table 2.—Young et al., 1996:514–516, Figs. 1a, 2b, d, e, m.—Feldman et al., 1997:271, 272, 275, Fig. 2, tables 1, 2.—Fisher et al., 1997:85, 88, 90, 91, table 1.—Miura et al., 1997: 455.—Julian et al., 1999:2245–2256.—

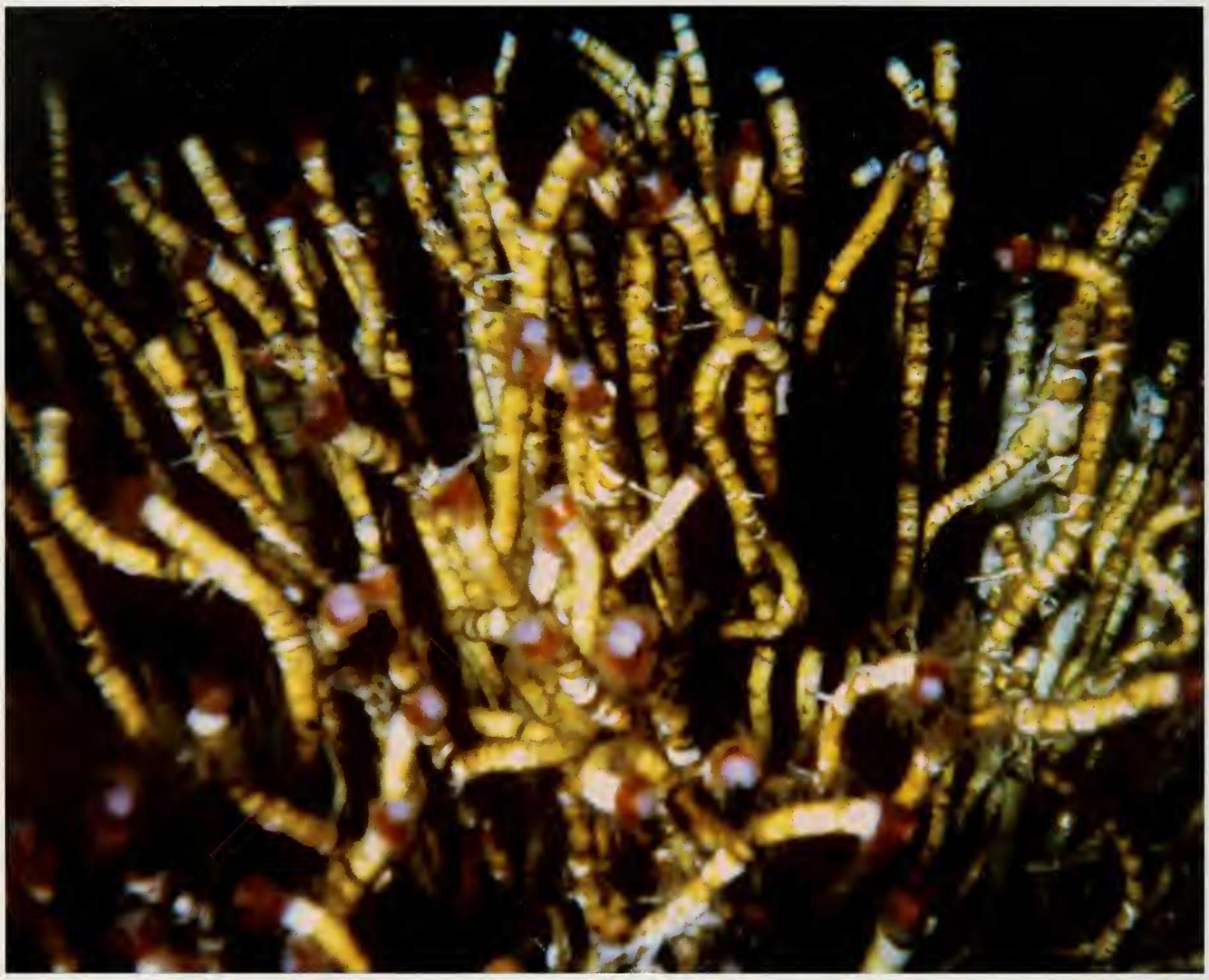

Fig. 1. In situ photograph of portion of large cluster of *Lamellibrachia luymesi* at Bush Hill hydrocarbon seep community. No scale.

Southward, 1999:196, Fig. 5.2, 5.4, 5.5.—Tyler & Young, 1999:196–198, 200–204, table 3.—Schulze, 2001:1–9, Figs. 1F, 2A, 4E, table 1.—Southward et al., 2002:1194.

Lamellibrachia barhami [not *Lamellibrachia barhami* Webb, 1969].—Fisher et al., 1988:232.

Undescribed species of *Lamellibrachia*.—Southward, 1991:872.

Lam.(GoM).—Williams et al., 1993:440, 443, Figs. 1–3, table 1.

L. sp.—Fisher, 1995:307, table 4.

Lamellibrachiid.—Fisher et al., 1997:86, 87, Figs. 1, 2.

Lamellibrachia sp. nov. 2.—Nelson & Fisher, 2000:4, 8, 10, Figs. 2, 3.

Lamellibrachia.—Salvini-Plawen, 2000: 133, 134.

Lamellibrachia cf. *luymesi*.—Freytag et al., 2001:13408–13412.—Gardiner et al., 2001:705.—Bergquist et al., 2002:89–98, Fig. 1.—McMullin et al., 2003: 8–31, Figs. 1, 2, 4, 5, tables 1, 2.

Material examined.—Twenty specimens, Green Canyon hydrocarbon seep community, 27°44.1′N, 91°15.3′W, *JSL I* dive 3523, 25 Jun 1993, 540 m, coll. C. R. Fisher; 8 specimens, Green Canyon hydrocarbon seep community, 27°44.1′N, 91°15.3′W, *JSL I* dive 3525, 26 Jun 1993, 540 m, coll. E. Nix; 12 specimens, Bush Hill hydrocarbon seep community, 27°47′N, 91°31.5′W, *JSL I* dive 3530, 28 Jun 1993, 540 m, coll. J. J. Childress. Selected specimens of this material are deposited in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.

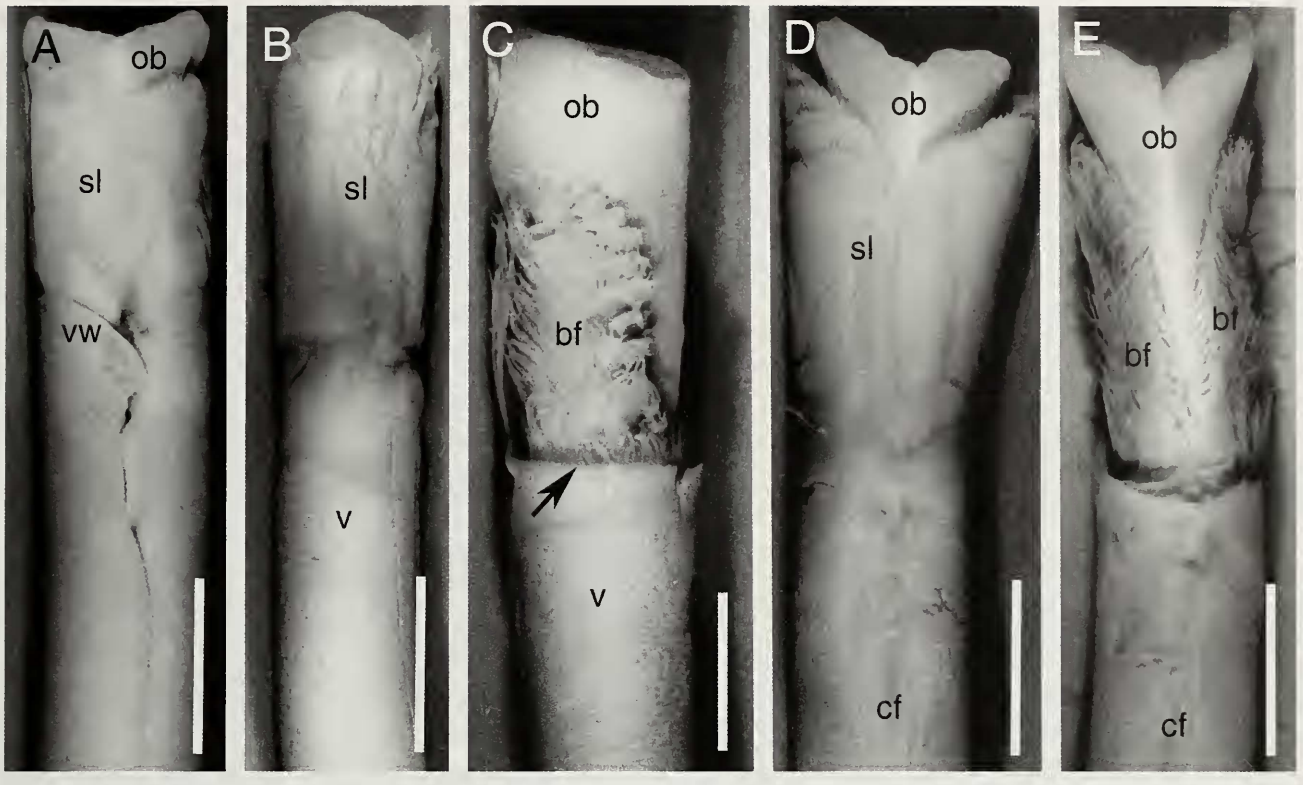

Fig. 2. *Lamellibrachia luymesi,* light micrographs of selected specimens. A, dorsal view of obturacular region showing sheath lamellae not extending to anterior face of obturaculum, together with portion of vestimental region with folded vestimental wings. B, left lateral view of obturacular region showing sheath lamellae nearly covering obturaculum, together with portion of vestimental region. C, right lateral view of obturacular region with sheath lamellae removed to show branchial filaments. Note extent of bare surfaces on obturaculum. Arrow indicates vestimental sheath around base of obturacular region. D, ventral view of obturacular region and portion of vestimental region. E, ventral view of obturacular region with sheath lamellae removed from both sides, exposing branchial filaments. bf, branchial filaments; cf, ciliated field; ob, obturaculum; sl, sheath lamellae; v, vestimental region; vw, vestimental wing. Scale bars: A, B, D, E = 5 mm; C = 3 mm.

Description.—Measurements of selected specimens (length by diameter, in mm; obturacular: vestimental: trunk: opisthosomal regions; + = incomplete; − = change in diameter; — = missing); (USNM 1007801): 9.4 by 4.5: 43 by 4: 142+ by 3.1: —; (USNM 1007803): 14.9 by 4.6: 56 by 4.7: 100+ by 2.3: —; (USNM 1007805): 16.3 by 5: 61.6 by 5.2: 110+ by 3.5: —; (USNM 1007807): 10.4 by 4.5: 51.5 by 4.2: 117+ by 3.4: —; (USNM 1007809): 7.8 by 4.4: 50.3 by 4.6: 115+ by 4.9: —. Measurements of selected tubes (length by diameter, in mm; + = incomplete, − = change in diameter): (USNM 1007801): 1340+ by 6.4–1.3; (USNM 1007802): 1560+ by 7.6–2.5; (USNM 1007804): 1405+ by 8.9–0.9; (USNM 1007806): 1230+ by 10.2–0.7; (USNM 1007808): 1190+ by 6.4–1.2.

Anterior face of obturaculum bare, without crust or secreted structures (Figs. 1, 2A–E). Obturaculum with 15–22 pairs of branchial lamellae ($\bar{X}$ = 17.8 ± 1.8; n = 10), composed of single type of filament (Fig. 2C, E), fused for most of length; free ends of filaments with two rows of pinnules and two rows of ciliated cells (Fig. 3A, B), pinnules on some filaments of unequal size (Fig. 3B); branchial lamellae typically covered by 4–8 sheath lamellae on each side of branchial crown ($\bar{X}$ = 5.3 ± 1.1; n = 30); number of sheath lamellae not directly correlated with size of specimen (Pearson's correlation); filaments of sheath lamellae lacking pinnules and cilia, almost completely fused, with very short free tips (Fig. 3C, D); sheath lamellae sometimes not extending to apical region of obturaculum (Fig. 2A, D). Distal surfaces of obturaculum of

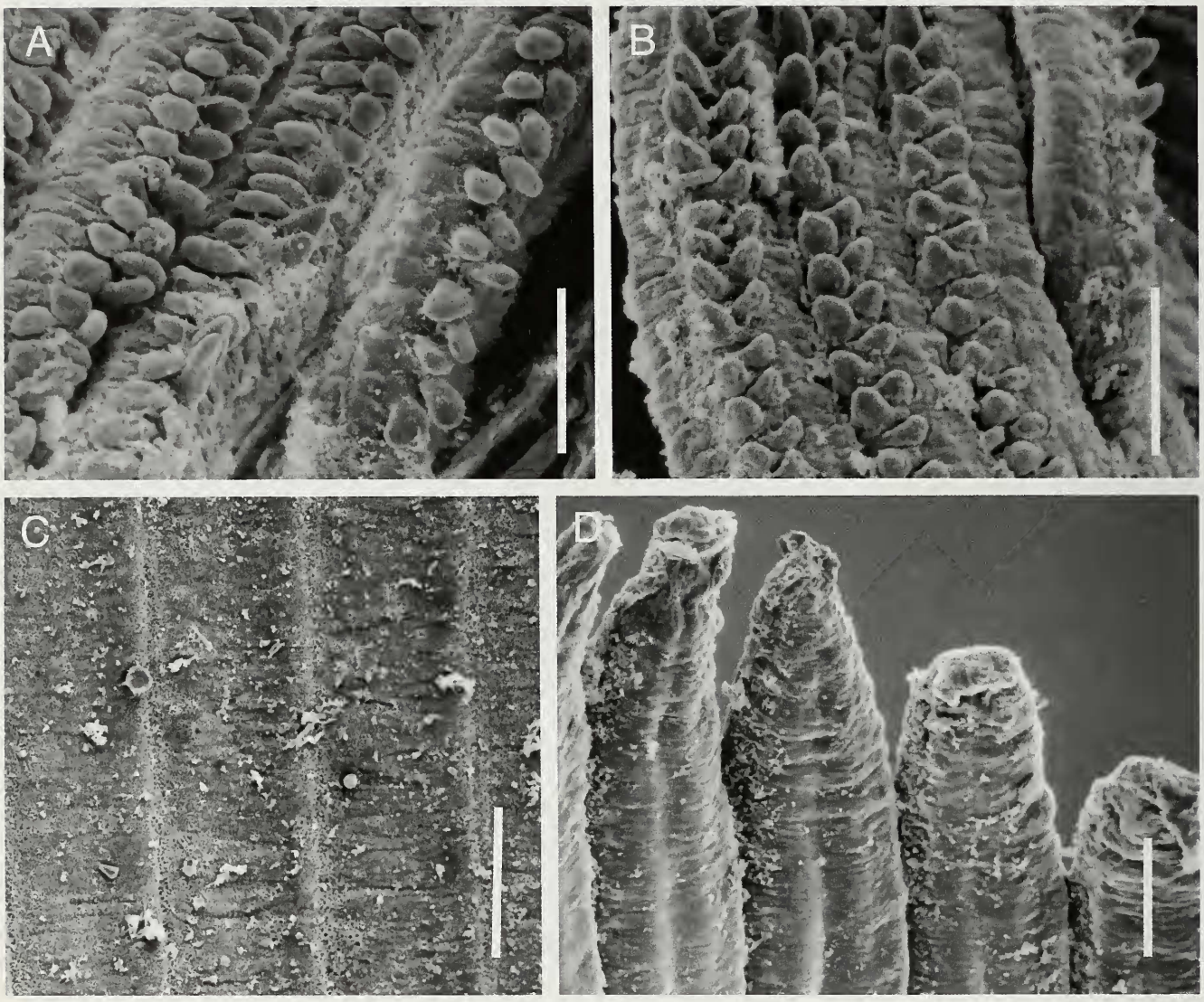

Fig. 3. *Lamellibrachia luymesi,* SEM. A, branchial filaments with pinnules of equal size. B, branchial filaments with pinnules of somewhat unequal size. C, inner face of fused filaments of sheath lamella. Note absence of pinnules and cilia. D, apical region of filaments of sheath lamella. Scale bars: A–C = 75 μm; D = 100 μm.

preserved specimens usually not concealed by branchial lamellae (Fig. 2C–E); obturaculum lenticular in cross-section (Fig. 4), lacking dorsal groove, with poorly developed ventral ridge distally; paired internal excretory ducts opening by single pore on dorsal surface at base of obturaculum; length of obturaculum from 6.6 to 16.3 mm ($\bar{X}$ = 10.8 ± 2.4 mm; n = 40); diameter of obturaculum from 3.4 to 5 mm; ($\bar{X}$ = 4.5 ± 0.6 mm; n = 40); ratio of obturacular length to vestimental length variable, 1:2.6 to 1:6.7 (n = 40). Anterior margin of vestimentum forming short sheath around base of obturaculum (Fig. 2C, arrow), with shallow mid-ventral incision usually with overlapping lobes; posteroventral margin of vestimentum discontinuous, with posteroventral lobes of variable size and separated by large gap (Fig. 5A, B); length of vestimentum from 26.9 to 61.6 mm ($\bar{X}$ = 47.2 ± 8.9 mm; n = 40); diameter of vestimentum from 3.7 to 5.2 mm ($\bar{X}$ = 4.3 ± 0.6 mm; n = 40); ratio of vestimental diameter to vestimental length highly variable, 1:6.2 to 1:16.4 (n = 40); ventral surface of vestimentum with ciliated field, wider in middle region, bluntly to sharply tapered at anterior and posterior ends (Figs. 2D, E, 5A, B); plaques associated with epidermis ventrally and laterally, increasing in density in posterior one-half of vestimentum (Fig. 5A, B, arrowheads); males with paired dorsal ciliated grooves extending from gonopores

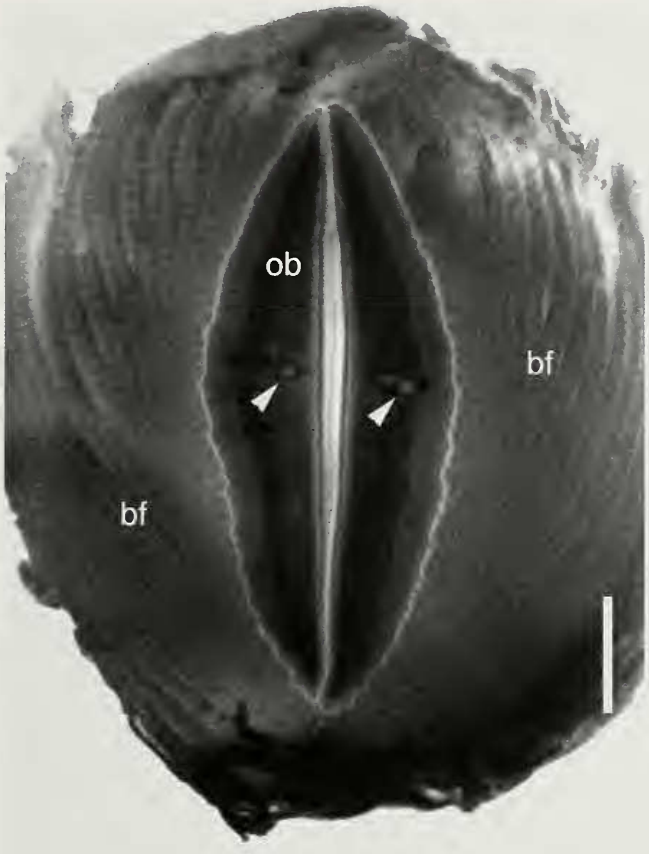

Fig. 4. *Lamellibrachia luymesi.* Light micrograph of cross section through middle region of branchial plume. Arrowheads indicate obturacular blood vessels. bf, branchial filaments; ob, obturaculum. Scale bar = 1 mm.

to near anterior end of vestimentum, diverging anteriorly (Fig. 5C). Trunk very long in adult specimens, tapering to less than 1 mm posteriorly; epidermis with numerous associated plaques 36–45 μm in diameter (Fig. 6). Opisthosome of selected specimen with 26 segments (Fig. 7A), 17 anterior segments each with chaetae occurring in single row, separated middorsally and midventrally by narrow band of epidermis lacking chaetae (Fig. 7B, C), and 9 posterior segments without chaetae; chaetae with teeth in anterior and posterior groupings; anterior grouping usually with 5 teeth in 2 rows, posterior grouping more variable, with 3–4 rows of 3–5 teeth (Fig. 7D). Tube hard, cream-colored to lightly yellowed tan with some dark banding anteriorly in living specimens (Fig. 1), becoming more darkly colored in preserved specimens; tube tapering posteriorly, diameter of aperture from 3.4 to 9.7 mm ($\bar{X}$ = 6.5 ± 1.5 mm, n = 44), with variable number of weakly to moderately developed collars anteriorly (Fig. 8A, B), becoming smooth in middle and posterior regions.

Distribution.—Presently known in the Atlantic Ocean from the type locality in 500 m of water off Guyana (8°01′N, 57°24′W) and in the Gulf of Mexico at several localities along the Louisiana slope in 500–650 m of water, including Green Canyon and Bush Hill hydrocarbon seep communities.

Remarks.—Several external morphological features have been used to distinguish between species of *Lamellibrachia,* including features of the branchial crown, proportions of body regions, and features of the tube (see Table 1). One of the most conspicuous features of the branchial crown is the presence of a number of sheaths composed of fused filaments, i.e., sheath lamellae, that enclose the inner branchial lamellae. Specimens of *L. luymesi* examined for this study usually possess 4 to 8 sheath lamellae on each side of the branchial crown, but most specimens have a different number of sheath lamellae on each side. Typically, one side will have 1 or 2 lamellae greater in number than the opposite side, although no pattern of preference is apparent in the specimens examined in this study. A few specimens have only 2 or 3 sheath lamellae on one side of the branchial crown. Close examination of the these specimens, however, always revealed damage to the branchial crown, and it is likely that some lamellae were torn away when the preserved specimens were removed from their tubes.

The number of pairs of sheath lamellae reported for the holotype of *L. luymesi* falls within the range recorded for specimens from the Gulf of Mexico and, therefore, supports their identification as *L. luymesi.* The majority of specimens with undamaged obturacula examined in the present study (23 of 30 specimens) exhibit a number of sheath lamellae intermediate between species with potentially fewer pairs (*L. barhami* and *L. satsuma*) and *L. columna* with

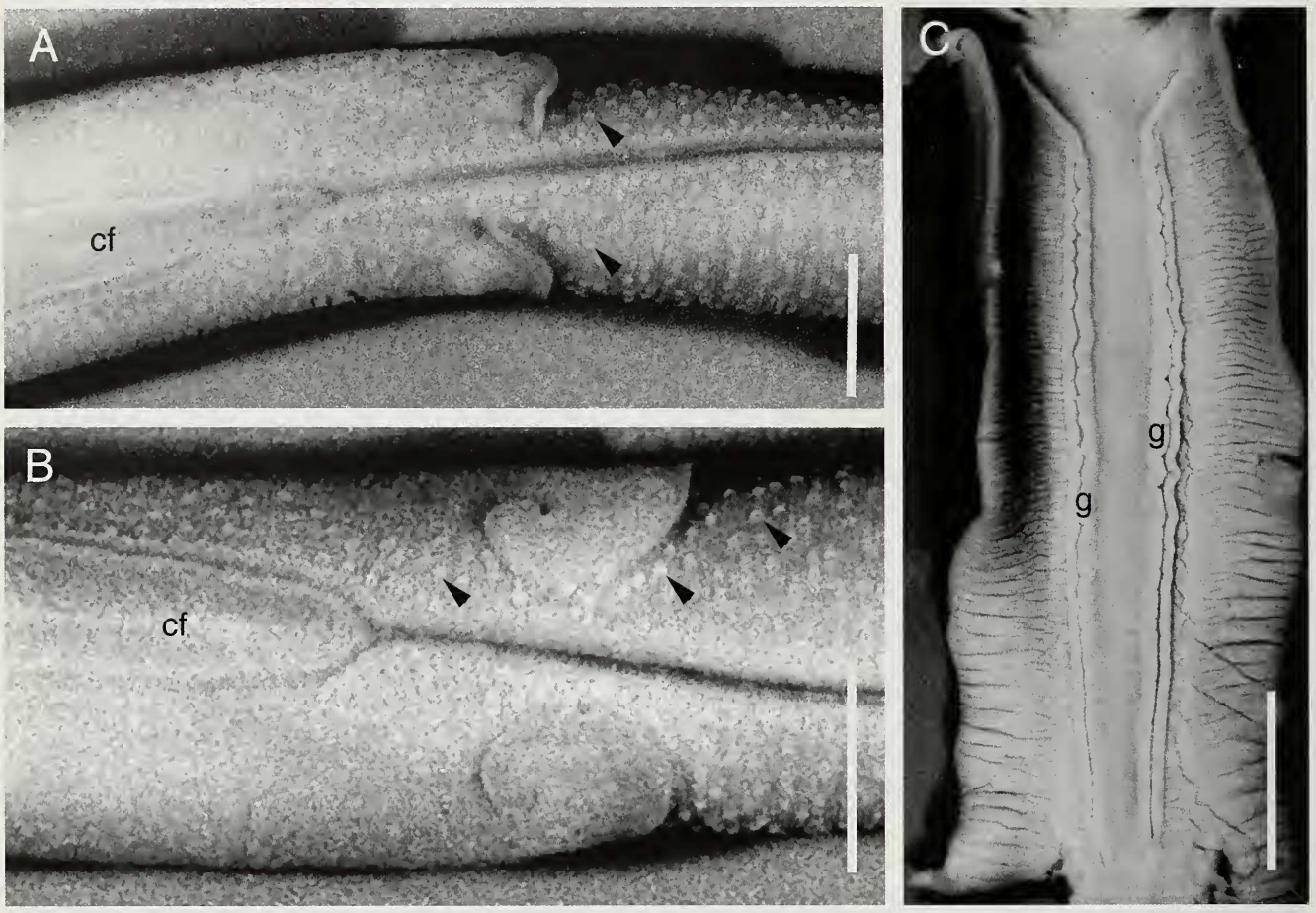

Fig. 5. *Lamellibrachia luymesi,* light micrographs of selected specimens. A, B, posterior end of vestimental region showing discontinuous posteroventral margin of vestimentum with variously developed lobes. Arrowheads indicate plaques on body wall. cf, ciliated field. C, dorsal view of vestimentum of male showing well-developed ciliated grooves (g) leading from gonopores to anterior end of vestimentum. Scale bars: A, B = 2 mm; C = 4 mm.

its higher number (Table 1). Number of pairs of sheath lamellae, therefore, is a useful character to distinguish *L. luymesi* from these other species. However, the number of sheath lamellae of the type material of *L. victori* falls within the range of *L. luymesi* so this character does not distinguish these two species.

Unlike the number of sheath lamellae, the number of branchial lamellae does not differ significantly so this feature is not a useful characteristic to distinguish between species (Table 1). Only *L. barhami* is reported to possess a number of branchial lamellae outside the range exhibited by specimens of *L. luymesi* examined in this study (see Webb 1969). However, Jones (1985) states that *L. barhami* can possess up to 25 pairs of branchial lamellae so it is likely that this species exhibits a range in number that is more consistent with other species of *Lamellibrachia.*

Although lengths and proportions of body regions are affected by a certain degree of contraction at the time of preservation, some interesting trends can be observed between species of *Lamellibrachia.* Among the five species of *Lamellibrachia* currently described, *L. columna* is the largest species and *L. satsuma* is potentially the smallest species (see Table 1). Lengths of the obturacular and vestimental regions of *L. barhami* overlap somewhat with those of *L. luymesi,* but the latter species exhibits a broader range of lengths for both regions and is generally overall the larger of the two species. The obturacular length reported for *L. victori* falls within the range of *L. luymesi* examined for this study, but its vestimental length is slightly greater than the

Fig. 6. *Lamellibrachia luymesi,* SEM. Portion of body wall of trunk region showing numerous plaques (p) and openings of pyriform glands (arrows). Scale bar = 100 μm.

maximum measured for *L. luymesi* (Table 1). Since the vestimental length of *L. victori* is based on a measurement taken from a single specimen, this difference is probably not significant.

Three species of *Lamellibrachia* for which multiple specimens have been examined, i.e., *L. barhami* (Webb 1969, Jones 1985), *L. luymesi* (present study), and *L. satsuma* (Miura et al. 1997), demonstrate generally similar ranges for the ratio of obturacular length to vestimental length (Table 1). Ratios calculated for the type material of *L. luymesi* and *L. victori* fall within the range observed for specimens of *L. luymesi* from the Gulf of Mexico.

When comparing ratios of vestimental diameter to vestimental length, *L. columna* and *L. luymesi* have generally similar values at the lower end of the range, but specimens of *L. luymesi* from the Gulf of Mexico exhibit a somewhat broader range overall (Table 1). Although the value calculated for the holotype of *L. luymesi* is slightly outside the range of specimens from the Gulf of Mexico, the value for that of *L. victori* falls within the range of *L. luymesi* from the Gulf of Mexico.

Van der Land & Nørrevang (1975, 1977) provide illustrations of the dorsal surface of the anterior region of the trunk of the holotype of *L. luymesi* that show a number of transverse grooves in the epidermis (they mistakenly state that these grooves occur on the ventral surface in their 1977 study; see p. 12). Southward (1991), however, questioned the taxonomic value of these grooves, suggesting that they may represent a contraction artifact. Specimens of *L. luymesi* from the Gulf of Mexico examined for this study vary greatly with regard to this feature. Some specimens possess numerous shallow grooves, whereas others have a few deep grooves, whereas still others lack grooves completely. We agree with Southward (1991) that these grooves, when present, represent an artifact of contraction produced at the time of preservation.

The opisthosome and opisthosomal chaetae are known for three species of *Lamellibrachia, L. luymesi* (present study), *L. columna* (Southward 1991) and *L. satsuma* (Miura et al. 1997). Although Webb (1969) discussed and illustrated what he thought was the opisthosome (= opisthomere in Webb) of four specimens of *L. barhami,* the absence of chaetae and external signs of segmentation cast doubt on his observations (also see Jones 1981). Southward (1991) suggested that the opisthosomal chaetae of vestimentiferans might display specific differences. Based on the limited chaetal material examined to date (one opisthosome each for *L. luymesi* and *L. satsuma,* and two for *L. columna*), significant specific differences among these species are not apparent. Chaetae possess teeth in anterior and posterior groupings in the following arrange-

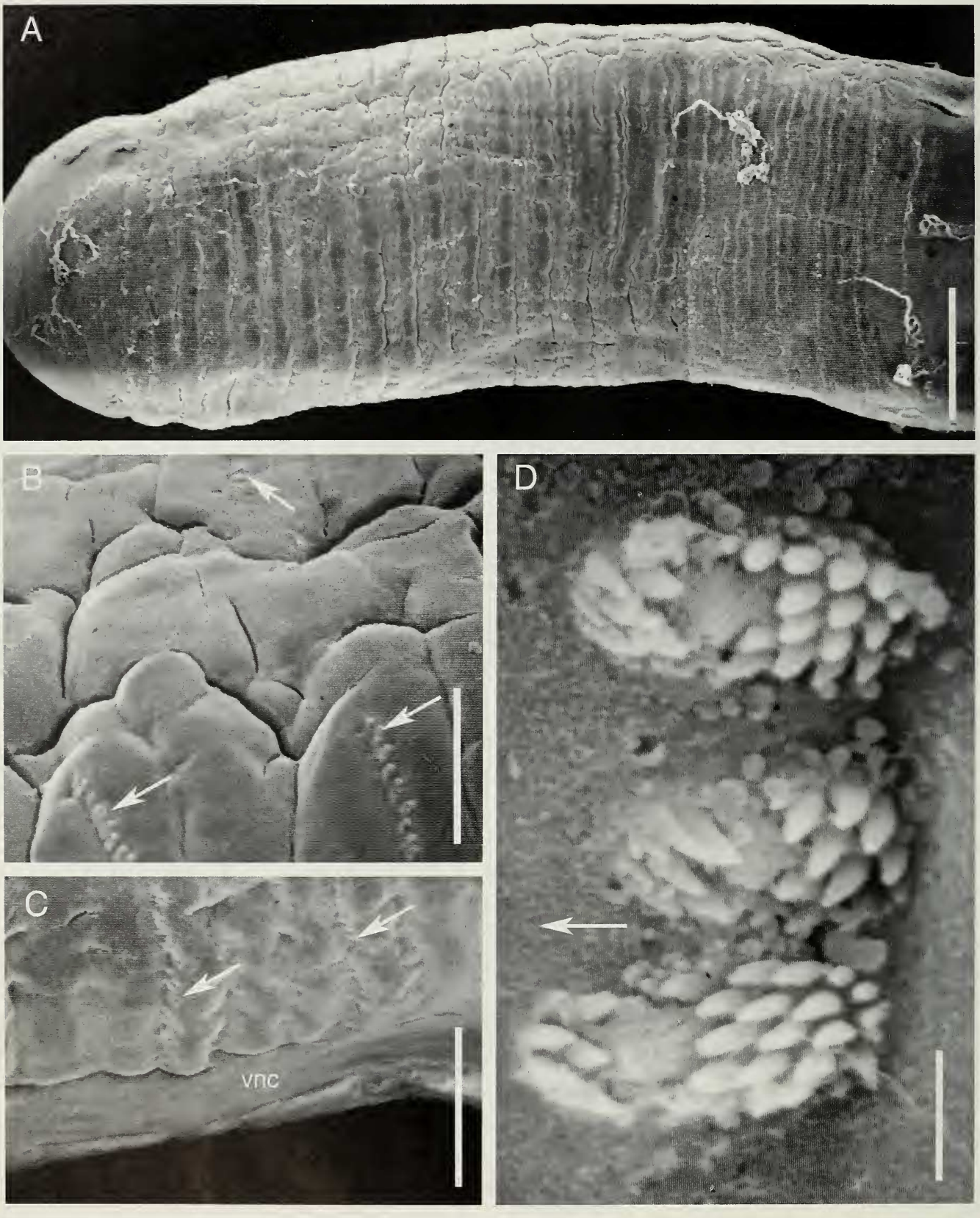

Fig. 7. *Lamellibrachia luymesi,* SEM of opisthosomal region. A, overview of opisthosome of selected specimen. B, dorsolateral view of two chaetigerous segments showing chaetae occurring in single rows (arrows) and middorsal area lacking chaetae. C, ventrolateral view of two chaetigerous segments showing chaetae (arrows) and position of internal ventral nerve cord (vnc). D, enlargement of chaetae. Arrow indicates anterior direction. Scale bars: A = 300 μm; B = 50 μm; C = 75 μm; D = 2 μm.

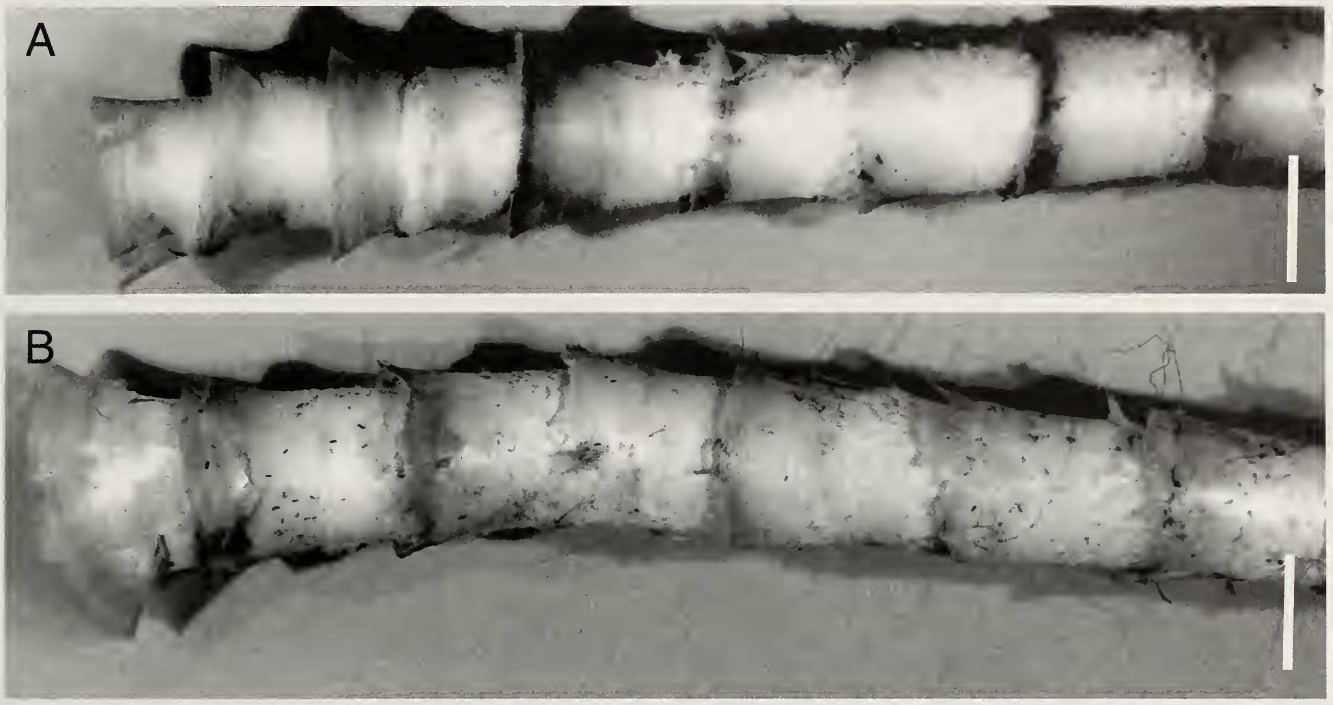

Fig. 8. *Lamellibrachia luymesi.* A, B, light micrographs of anterior ends of tubes showing growth collars. Scale bars = 5 mm.

ments for *L. luymesi, L. columna,* and *L. satsuma,* respectively: anterior groupings—5 teeth in 2 rows, 2–7 teeth in 1–2 rows, 6–9 teeth in 2 rows; posterior groupings—3–4 rows of 3–5 teeth, 3–5 rows of 3–4 teeth, 3–4 rows of 3–4 teeth. Some differences in the number of teeth in each grouping and the number of rows in which they occur exist between these species. However, additional material should be examined to quantify better any possible differences in chaetal characteristics of these and other species of *Lamellibrachia.*

With the possible exception of the maximum tube length provided for *L. satsuma,* tube lengths of all species listed in Table 1 are of incomplete tubes so the full extent of possible tube length in most species of *Lamellibrachia* is uncertain at this time. For *L. luymesi* in the Gulf of Mexico, tube lengths may actually exceed 2 m (SLG, SH, pers. obs.). Based on the absence of discoloration in the posterior region of the tube, van der Land & Nørrevang (1975, 1977) suggested that the tube of the holotype of *L. luymesi* was not buried in sediment. In contrast, specimens of *L. luymesi* in the Gulf of Mexico may have one-half or more of their tube length buried in sediment (SLG, SH, pers. obs.). Van der Land & Nørrevang (1975, 1977) acknowledged that the tube of the holotype of *L. luymesi* was incomplete posteriorly. Based on our observations of *L. luymesi* in the Gulf of Mexico, we believe that the tube of the holotype was broken at the time of collection, leaving a posterior portion buried in sediment.

The presence of collars on the anterior region of tubes is a common feature among vestimentiferans so it is not a particularly useful character to distinguish between species. It is interesting to note, however, that among the five described species of *Lamellibrachia, L. columna* is unique in lacking such collars on its tubes (Southward 1991).

Status of Lamellibrachia victori.—In her comparison of species of *Lamellibrachia* known at the time, Southward (1991) concluded that *L. columna* and *L. barhami* were distinct from each other and that both species were different from *L. luymesi* and *L. victori.* She further noted, however, that *L. luymesi* and *L. victori* could not be clearly distinguished from each other, but the limited material available for each species at the time hindered comparisons. Although

Table 1.—Comparison of certain diagnostic characters for species of *Lamellibrachia*.

	n	Number of sheath lamellae	Number of branchial lamellae	Obturaculum length (mm)	Vestimentum length (mm)	Obturaculum length: vestimentum length	Vestimentum diameter: vestimentum length	Tube length (mm; max)	Tube diameter (mm; aperture)
L. luymesi Gulf of Mexico specimens	40	4–8[a]	15–22	6.6–16.3	26.9–61.6	1:2.6 to 1:6.7	1:6.2 to 1:16.4	1560	3.4–9.7
L. luymesi, holotype van der Land & Nørrevang, 1975	1	6	19[b]	13	63	1:4.8	1:4.5	687	10
L. barhami Webb, 1969	>15[c]	2–4	25	4.5–12.2	23–36.5	1:2.5 to 1:7.8	1:2.9 to 1:6.7	1546	7.5–9
L. victori Mañé-Garzón & Montero, 1985	2	7	18[d]	13	65	1:5	1:8	240	15
L. columna Southward, 1991	14	8–16	21[e]	15–42	60–120	1:2.2 to 1:4.5	1:6.5 to 1:13	820	14–20
L. satsuma Miura, Tsukahara & Hashimoto, 1997	82	0–4[f]	up to 19	1.8–9.8	7.2–24	1:2.1 to 1:8.3	—	1000	2.5–8.7

[a] Undamaged specimens.
[b] Approximate number from Fig. 18 in van der Land & Nørrevang (1977).
[c] Four type specimens from Webb (1969) and numerous specimens from Jones (1985).
[d] Approximate number from Fig. 6 in Mañé-Garzón & Montero (1985).
[e] Approximate number from Fig. 5B in Southward (1991).
[f] Zero in juvenile specimens.

no publications to date indicate that new material of *L. victori* has been collected, abundant new material of *L. luymesi* from the Gulf of Mexico has been examined in the present study, allowing for a better understanding of the morphological variation it exhibits for a number of external features (see Table 1). Results of this study corroborate Southward's (1991) conclusion that *L. luymesi* is distinct from other species of *Lamellibrachia,* except for *L. victori.* For all features listed in Table 1, values for the type material of *L. victori* fall within the range of *L. luymesi* (holotype and Gulf of Mexico specimens), except for length of the vestimentum and aperture diameter of the tube. Because values for these features of *L. victori* are taken from a very limited number of specimens, it is difficult to know their significance with regard to recognizing *L. victori* as a valid species of *Lamellibrachia.* It is likely, however, that the difference in vestimental length is not significant. To resolve this issue, new material must be obtained from the area where the type material of *L. victori* was collected and compared with *L. luymesi.* Until such a study is completed, *L. victori* remains questionably distinct from *L. luymesi.*

Discussion

Presently, ten genera of vestimentiferan tube worms have been described, including *Lamellibrachia* Webb, 1969, *Riftia* Jones, 1981, *Escarpia* Jones, 1985, *Oasisia* Jones, 1985, *Ridgeia* Jones, 1985, *Tevnia* Jones, 1985, *Alaysia* Southward, 1991, *Arcovestia* Southward & Galkin, 1997, *Seepiophila* Gardiner, McMullin & Fisher, 2001, and *Paraescarpia* Southward, Schulze & Tunnicliffe, 2002. With five described species, *Lamellibrachia* contains the largest number of species of these genera. *Escarpia* contains two recognized species, whereas all other genera are monotypic. Among these genera, *Lamellibrachia* also demonstrates the broadest geographic range with two described species occurring in the western Pacific Ocean (*L. columna* and *L. satsuma*), one species in the eastern Pacific Ocean (*L. barhami*), and two species in the western Atlantic Ocean, including the Gulf of Mexico (*L. luymesi* and *L. victori*). Dando et al. (1992) found tubes of vestimentiferan worms in a shipwreck in 1160 m of water in the eastern Atlantic Ocean off Vigo, Spain. They indicated that the appearance of the tubes resembled that of tubes of *L. barhami,* but they were unable to confirm the identity of the species because fully intact worms were not available. Williams et al. (1993), however, were able to obtain degraded tissue from these tubes. In their analysis of the 28S rRNA nuclear gene, they demonstrated that this tissue consistently grouped with species of *Lamellibrachia* also examined in their study. This finding supports the suggestion that the tubes belong to a species of *Lamellibrachia,* thereby confirming the presence of *Lamellibrachia* in the eastern Atlantic Ocean. Recently, *Lamellibrachia* was reported from the southeastern Mediterranean Sea off Crete and Turkey in about 1700 to 2000 m of water (Olu-Le Roy et al. 2001). Currently, no vestimentiferan species are known to occur in the Indian Ocean (see Van Dover et al. 2001).

The two Atlantic species of *Lamellibrachia* are presently known only from cold seep regions on continental margins. It is of interest to note that two Pacific species, i.e., *L. barhami* and *L. satsuma,* have been collected from vent and seep sites, whereas a third described Pacific species, *L. columna,* is recorded only from vent sites (Southward & Galkin 1997, Tunnicliffe et al. 1998, Kojima et al. 2001). In a study based on a partial nucleotide sequence of the cytochrome oxidase I mitochondrial gene (COI) of specimens of *Lamellibrachia* collected from ten sites in the western Pacific, Kojima et al. (2001) recognized four tentative undescribed species, in addition to specimens identified as *L. satsuma.* Of these four undescribed species, two were collected from vent sites only, one was found exclu-

sively in seep sites, and one occurred in vent and seep sites.

Among species of *Lamellibrachia* presently described, morphological characters of the specimens examined in this study are consistent with those of *L. luymesi* and *L. victori.* If these two species are shown to be identical in the future, *L. luymesi* has priority. However, the type locality of *L. luymesi* off Guyana and localities in the northern Gulf of Mexico where specimens were collected for the present study are separated by a distance of approximately 4000 km with localities of intermediate populations not currently known. Based on sequence similarity of the COI mitochondrial gene, McMullin et al. (2003) report that populations of a species of *Lamellibrachia,* which occur over a distance of 6000 km along the west coast of North America, represent a single species, i.e., *L. barhami.* Using similar evidence, McMullin et al. (2003) also indicate that *Paraescarpia echinospica* exhibits a geographic range of at least 4500 km in the western Pacific Ocean. Based on morphological similarity, we suggest that *L. luymesi* is distributed over a wide geographic range in the western Atlantic Ocean.

Lamellibrachia luymesi co-occurs in the Gulf of Mexico with two additional vestimentiferan worms, *Seepiophila jonesi,* which is sympatric with *L. luymesi* in certain seep communities (see Gardiner et al. 2001), and *Escarpia laminata* which was originally recorded from deep water at the base of the Florida Escarpment (Paull et al. 1984, Jones 1985). In addition to the seep sites reported in this study, a species of *Lamellibrachia* occurs along the Louisiana slope in the Gulf of Mexico in a large number of other seep sites (see references in synonymy above for coordinates), extending along a distance of at least 480 km and depths of 550 to 650 m of water. An analysis of the COI gene of specimens taken from populations of *Lamellibrachia* along this distance of the Louisiana slope, including the seep sites used for this study, shows genetic distances indicative of intraspecific variation (McMullin et al. 2003). Morphological similarity of specimens examined in this study, together with the evidence from the analysis of the COI gene, support the suggestion that a single species of *Lamellibrachia,* i.e., *L. luymesi,* inhabits hydrocarbon seep communities along the Louisiana slope in the Gulf of Mexico.

Acknowledgments

This work was supported by the NOAA National Undersea Research Program at the University of North Carolina, Wilmington, Harbor Branch Oceanographic Institution, National Science Foundation OCE 0117050 to C. R. Fisher, and the Minerals Management Service, Gulf of Mexico Regional OCS Office through the contract number 1435-10-96-CT30813 to C. R. Fisher. We thank the captain and crew of the RV *Edwin Link* and the submersible crew and pilots of the *Johnson-Sea-Link.* We thank Erica Nix, Jim Childress and Chuck Fisher for collecting and providing specimens and Dr. James Sidie and Dr. A. C. Allen of Ursinus College for making their SEM facilities available for our use. We thank Laura Sharkey and Adam Dewan, undergraduate students of Bryn Mawr College and Haverford College, respectively, for their assistance in obtaining and analyzing morphometric data used in this study. The senior author extends special appreciation to Chuck Fisher, The Pennsylvania State University, for providing ship time and submersible time on several cruises in the Gulf of Mexico.

Literature Cited

Bergquist, D. C., I. A. Urcuyo, & C. R. Fisher. 2002. Establishment and persistence of seep vestimentiferan aggregations on the upper Louisiana slope of the Gulf of Mexico.—Marine Ecology Progress Series 241:89–98.

Brooks, J. M., et al. 1987. Deep-sea hydrocarbon seep communities: evidence for energy and nutritional carbon sources.—Science 238:1138–1142.

Carney, R. S. 1994. Consideration of the oasis analogy for chemosynthetic communities at Gulf of

Mexico hydrocarbon vents.—Geo-Marine Letters 14:149–159.

Childress, J. J., & C. R. Fisher. 1992. The biology of hydrothermal vent animals: physiology, biochemistry, and autotrophic symbioses. Pp. 337–441 *in* M. Barnes, A. D. Ansell, & R. N. Gibson, eds., Oceanography and Marine Biology An Annual Review, vol. 30. Biddles Ltd, King's Lynn and Guilford, England, 627 pp.

———, ———, J. M. Brooks, M. C. Kennicutt, II, R. Bidigare, & A. E. Anderson. 1986. A methanotrophic marine molluscan (Bivalvia: Mytilidae) symbiosis: mussels fueled by gas.—Science 233:1306–1308.

Dando, P. R., A. J. Southward, E. C. Southward, D. R. Dixon, A. Crawford, & M. Crawford. 1992. Shipwrecked tube worms.—Nature 356:667.

Feldman, R. A., M. B. Black, C. S. Cary, R. A. Lutz, & R. C. Vrijenhoek. 1997. Molecular phylogenetics of bacterial endosymbionts and their vestimentiferan hosts.—Molecular Marine Biology and Biotechnology 6:268–277.

Fisher, C. R. 1995. Toward an appreciation of hydrothermal-vent animals: their environment, physiological ecology, and tissue stable isotope values. Pp. 297–316 *in* S. E. Humphris, R. A. Zierenberg, L. S. Mullineaux, & R. E. Thomson, eds., Seafloor hydrothermal systems: physical, chemical, biological, and geochemical interactions. Geophysical Monographs Series 91:1–466.

———, J. J. Childress, & N. K. Sanders. 1988. The role of vestimentiferan hemoglobin in providing an environment suitable for chemoautotrophic sulfide oxidizing endosymbionts.—Symbiosis 5:229–246.

———, M. C. Kennicutt, II, & J. M. Brooks. 1990. Stable carbon isotopic evidence for carbon limitation in hydrothermal vent vestimentiferans.—Science 247:1094–1096.

———, I. A. Urcuyo, M. A. Simpkins, & E. Nix. 1997. Life in the slow lane: growth and longevity of cold-seep vestimentiferans.—Marine Ecology 18:83–94.

Freytag, J. K., P. R. Girguis, D. C. Bergquist, J. P. Andras, J. J. Childress, & C. R. Fisher. 2001. A paradox resolved: sulfide acquisition by roots of seep tubeworms sustains net chemoautotrophy.—Proceedings of the National Academy of Sciences 98:13408–13413.

Gardiner, S. L., E. McMullin, & C. R. Fisher. 2001. *Seepiophila jonesi,* a new genus and species of vestimentiferan tube worm (Annelida: Pogonophora) from hydrocarbon seep communities in the Gulf of Mexico.—Proceedings of the Biological Society of Washington 114:694–707.

Jones, M. L. 1981. *Riftia pachyptila,* new genus, new species, the vestimentiferan worm from the Galápagos Rift geothermal vents (Pogonophora).—Proceedings of the Biological Society of Washington 93:1295–1313.

———. 1985. On the Vestimentifera, new phylum: six new species, and other taxa, from hydrothermal vents and elsewhere.—Bulletin of the Biological Society of Washington 6:117–158.

Julian, D., F. Gaill, E. Wood, A. J. Arp, & C. R. Fisher. 1999. Roots as a site of hydrogen sulfide uptake in the hydrocarbon seep vestimentiferan *Lamellibrachia* sp.—The Journal of Experimental Biology 202:2245–2257.

Kennicutt, M. C., II, J. M. Brooks, R. R. Bidigare, R. R. Fay, T. L. Wade, & T. J. McDonald. 1985. Vent-type taxa in a hydrocarbon seep region on the Louisiana slope.—Nature 317:351–353.

Kojima, S., S. Ohta, T. Yamamoto, T. Miura, Y. Fujiwara, & J. Hashimoto. 2001. Molecular taxonomy of vestimentiferans of the western Pacific and their phylogenetic relationship to species of the eastern Pacific. I. Family Lamellibrachiidae.—Marine Biology 139:211–219.

Land, J. van der, & A. Nørrevang. 1975. The systematic position of Lamellibrachia [sic] (Annelida, Vestimentifera). Pp. 86–101 *in* A. Nørrevang ed., The phylogeny and systematic position of Pogonophora. Zeitschrift für zoologische Systematik und Evolutionsforshung, Sonderheft 1, 143 pp.

———, & ———. 1977. Structure and relationships of *Lamellibrachia* (Annelida, Vestimentifera).—Det Kongelige Danske Videnskabernes Selskab, Biologiske Skrifter 21(3):1–102.

MacDonald, I. R., G. S. Boland, J. S. Baker, J. M. Brooks, M. C. Kennicutt, II, & R. R. Bidigare. 1989. Gulf of Mexico hydrocarbon seep communities II. Spatial distribution of seep organisms and hydrocarbons at Bush Hill.—Marine Biology 101:235–247.

———, N. L. Guinasso, Jr., J. F. Reilly, J. M. Brooks, W. R. Callender, & S. G. Gabrielle. 1990. Gulf of Mexico hydrocarbon seep communities: VI. Patterns in community structure and habitat.—Geo-Marine Letters 10:244–252.

Mañé-Garzón, F., & R. Montero. 1985. Sobre una nueva forma de verme tubicola Lamellibrachia victori [sic] n.sp. (Vestimentifera)–Proposicion de un nuevo phylum: Mesoneurophora.—Revista de Biologia del Uruguay 8:1–28.

McMullin, E. R., S. Hourdez, S. W. Schaeffer, & C. R. Fisher. 2003. Phylogenetics and biogeography of deep-sea vestimentiferan tubeworms and their bacterial symbionts.—Symbiosis 34:1–41.

Miura, T., J. Tsukahara, & J. Hashimoto. 1997. *Lamellibrachia satsuma,* a new species of vestimentiferan worms (Annelida: Pogonophora) from a shallow hydrothermal vent in Kagoshi-

ma Bay, Japan.—Proceedings of the Biological Society of Washington 110:447–456.

Nelson, K., & C. R. Fisher. 2000. Absence of cospeciation in deep-sea vestimentiferan tube worms and their bacterial endosymbionts.—Symbiosis 28:1–15.

Olu-Le Roy, K., M. Sibuet, G. Levitre, S. Gofas, & A. Fiala-Médioni. 2001. Cold seep communities in the deep Mediterranean Sea (South of Crete and Turkey): faunistic composition and spatial distribution.—Program and abstracts. Second International Symposium on Deep-sea Hydrothermal Vent Biology. Brest, France. [Abstract, p. 208].

Paull, C. K., et al. 1984. Biological communities at the Florida Escarpment resemble hydrothermal vent taxa.—Science 226:965–967.

Salvini-Plawen, L. V. 2000. What is convergent/homoplastic in Pogonophora?—Journal of Zoological Systematics & Evolutionary Research 38:133–147.

Schulze, A. 2001. Comparative anatomy of excretory organs in vestimentiferan tube worms (Pogonophora, Obturata).—Journal of Morphology 250:1–11.

Scott, K. M., & C. R. Fisher. 1995. Physiological ecology of sulfide metabolism in hydrothermal vent and cold seep vesicomyid clams and vestimentiferan tube worms.—American Zoologist 35: 102–111.

Southward, E. C. 1991. Three new species of Pogonophora, including two vestimentiferans, from hydrothermal sites in the Lau Back-arc Basin (Southwest Pacific).—Journal of Natural History 25:859–881.

———. 1999. Development of Perviata and Vestimentifera (Pogonophora).—Hydrobiologia 402: 185–202.

———, & S. V. Galkin. 1997. A new vestimentiferan (Pogonophora: Obturata) from the hydrothermal vent fields in the Manus Back-arc Basin (Bismarck Sea, Papua New Guinea, Southwest Pacific Ocean).—Journal of Natural History 31: 43–55.

———, A. Schulze, & S. L. Gardiner. 2003. Pogonophora: form and function (Annelida).—Hydrobiologia (in press).

———, ———, & V. Tunnicliffe. 2002. Vestimentiferans (Pogonophora) in the Pacific and Indian Oceans: a new genus from Lihir Island (Papua New Guinea) and the Java Trench, with the first report of *Arcovestia ivanovi* from the North Fiji Basin.—Journal of Natural History 36:1179–1197.

Tunnicliffe, V., A. G. McArthur, & D. McHugh. 1998. A biogeographical perspective of the deep-sea hydrothermal vent fauna.—Advances in Marine Biology 34:353–442.

Tyler, P. A., & C. M. Young. 1999. Reproduction and dispersal at vents and cold seeps.—Journal of the Marine Biological Association, United Kingdom 79:193–208.

Van Dover, C. L., et al. 2001. Biogeography and ecological setting of Indian Ocean hydrothermal vents.—Science 294:818–823.

Webb, M. 1969. *Lamellibrachia barhami*, gen. nov., sp. nov. (Pogonophora), from the Northeast Pacific.—Bulletin of Marine Science 19:18–47.

Williams, N. A., D. R. Dixon, E. C. Southward, & P. H. W. Holland. 1993. Molecular evolution and diversification of the vestimentiferan tube worms.—Journal of the Marine Biological Association, United Kingdom 73:437–452.

Young, C. M., E. Vázquez, A. Metaxas, & P. A. Tyler. 1996. Embryology of vestimentiferan tube worms from deep-sea methane/sulfide seeps.—Nature 381:514–516.